

The Evolutionary Significance of Learning: what the ‘Baldwin Effect’ Dialogue Failed to Appreciate

Abstract The idea that evolution is partly directed by learning has been debated under the assumption that what is meant by this is learned behavior becoming hereditary (instinctive) behavior over time, a phenomenon called the ‘Baldwin effect’. I argue that there is a very simple and compelling reason to grant learning an essential role in shaping evolutionary history. However, despite the preoccupation with the Baldwin effect, this reason has nothing to do, *per se*, with what becomes of the learned behavior itself. The position I propose is not unprecedented. Not only is it implicit in some of the Baldwin effect literature itself, it has also been well developed in a very different context to discussions about learning: in Ernst Mayr’s views on evolutionary novelty. But while this significance of learning is evident enough from a Modern Synthesis starting point, it also touches on the more radical developmentalist views of Gottlieb (2002) and West-Eberhard (2003).

Keywords Learning, Behavior, Evolution, Baldwin Effect, Mayr, West-Eberhard

1. Introduction

In recent decades there has been a considerable amount of discussion over the capacity of learning to direct the course of evolution. The nominal topic of this discussion is the so-called ‘Baldwin effect’, a term coined by George Gaylord Simpson. For Simpson, “the essence” of this concept is that “[c]haracters individually acquired by members of a group of organisms may eventually, under the influence of selection, be reinforced or replaced by similar hereditary characters” (1953, p. 110). This clearly states that the character in question undergoes two distinct processes. First, it is ‘individually acquired’, and second, its acquired form is ‘reinforced or replaced’ by an hereditary one. From here on I shall refer to these processes as ‘individual acquisition’ and ‘hereditary replacement’.

It is the hereditary replacement element that discussion about the Baldwin effect is fundamentally about. The Baldwin effect is controversial because hereditary replacement bears a superficial resemblance to Lamarckism. The significance of learning (i.e. individual acquisition) for evolution is presented as a potential expansion or even critique of traditional evolutionary theory, but only inasmuch as it can lead to hereditary replacement. In this way, the significance of learning has been conflated with that of hereditary replacement, and thus with the Baldwin effect. Consequently, discussion of learning and evolution has been focused on hereditary replacement, under the assumption that it is the place to look for a novel evolutionary principle. This implies that individual acquisition is not of special importance in its own right.

To the contrary, I hope to show that a proper consideration of individual acquisition and its consequences reveals a key role for learning that is essential for understanding the evolution of life. Basically, learned behavior *does* significantly influence evolution, whether it undergoes hereditary replacement (and hence a Baldwin effect) or not. In this way, a straightforward and compelling reason for seeing learning as an evolutionary mechanism has been missed in the one major recent dialogue about that very issue, and remains neglected.

This argument will be made in two parts. The first part revisits some of the key texts on the Baldwin effect to reveal the extent to which an individual acquisition centred argument for learning already exists in this literature. I then show that the same argument has, in fact, been made in a context far removed from rhetoric about learning: the macroevolutionary views of Ernst Mayr. This extant argument has obvious implications for evolutionary theory. The second part brings the individual acquisition argument up to date to show how much further it can be taken. After freeing the argument from the conservative framework of Mayr, its implications are extended by the theory of Gottlieb (2002). Finally, the focus on learning

and behavior is placed in the broader context of phenotypic plasticity, the evolutionary perspective advocated by West-Eberhard (2003).

I therefore consider the role of learning in evolution from both the Modern Synthesis and post-Modern Synthesis perspectives. In doing so, I hope to convey a point that the logic of the importance of learning is so simple that the argument works either way. That being said, I also suggest an open question regarding its implications for the Modern Synthesis and how we conceive of it. It relates to the Modern Synthesis tradition of dismissing non-hereditary traits in individuals.

2. Individual Acquisition from Baldwin to Mayr

In perhaps his most widely cited work on what would come to be called the ‘Baldwin effect’, Baldwin conveniently divides his discussion between ontogeny and phylogeny. It is in the first category that he defines ‘organic selection’ as “the organism’s behavior in acquiring new modes or modifications of adaptive function with its influence of structure” (1896, p. 444). Here is Baldwin’s term for ‘individual acquisition’. In phylogeny, organic selection “secures by survival certain lines of determinate phylogenetic variation in the directions of the determinate ontogenetic adaptations of the earlier generation” (p. 447, original in italics). In other words, the beneficial ‘directions’ of traits that were previously acquired are ‘secured’ by those same ‘directions’ of traits later becoming phylogenetic i.e. hereditary. Baldwin is describing ‘hereditary replacement’, thus confirming Simpson’s interpretation. In the quote above, ‘organic selection’ refers to individual acquisition. However, in the concluding section of the same paper, Baldwin expands the definition to “[t]he process of ontogenetic adaptation considered as keeping single organisms alive *and so securing determinate lines of variation in subsequent generations*” (p. 552, emphasis added). This incorporates hereditary replacement, and thus is Baldwin’s own term for the ‘Baldwin

effect', and the understanding accepted in the modern literature. The inconsistency reflects his redefinition of organic selection from individual acquisition in earlier works to the 'new factor' (the Baldwin effect).ⁱ

Lloyd Morgan's account is very similar: "In addition to what is congenitally definite in structure or mode of response, an organism inherits a certain amount of innate modifiability or plasticity" (1896, p. 739). The resulting modifications are Lloyd Morgan's individual acquisitions. Furthermore, "Any congenital variations similar in direction to these modifications will tend to support them and to favour the individuals in which they occur... Thus will arise a congenital predisposition to the modifications in question" (p. 740). Hereditary replacement, and echoing Baldwin's words.

An important difference between Baldwin and Lloyd Morgan here is that Baldwin has a focus on cognitive phenomena that Lloyd Morgan does not. While 'organic selection' involves both physical and psychological phenomena, its function as Baldwin's 'new factor' in evolution is effective through the psychological avenue: "The intelligence which is appealed to, to take the place of instinct and to give rise to it, uses just these partial variations which tend in the direction of the instinct" (Baldwin, p. 446). For this reason, a particular focus on Baldwin's version of the Baldwin effect may be justified if one is especially concerned with learning.

In a commonly cited passage, Baldwin lays down the essential, fundamental starting point of his argument, namely the environment:

The creatures which can stand the "storm and stress" of the physical influences of the environment, and of the changes which occur in the environment, *by undergoing modifications of their congenital functions or of the structures which they get congenitally-these creatures will live; while those which cannot, will not* (p. 445, author's own emphasis).

There are two things in this passage that deserve our attention. The first is a fairly trivial qualification. Other commentators have noted how these ‘creatures’ in Baldwin’s eyes either live or die according to their capacity for modification. In Modern Synthesis thinking selection does not operate in terms of a digital ‘live or die’ mechanism, but rather in degrees of fitness as distributed across populations, such that those of low fitness need not perish, but as a group are outcompeted by their genetically superior rivals. In Baldwin’s time, however, his repetitive reference to ‘keeping the organism alive’ is rather typical of current thinking, what has been called ‘the fly-swatter theory of natural selection’ (Depew, 2003, pp. 10-11).ⁱⁱ It would be prudent to keep this distinction in mind when considering seriously the argument under discussion.

The second point to highlight from Baldwin is summed up in the word ‘changes’. Baldwin is approaching evolution from the perspective of changing environments and the challenges they pose to environment adapted (and thereby dependent) life forms. As is often the case, Lloyd Morgan makes the point much more explicit:

But now suppose that the conditions of the environment somewhat rapidly change... Here individual plasticity steps in to save some of the members of the race from extinction. They adapt themselves to the changed conditions through a modification of the bodily tissues (Lloyd Morgan, p. 738).

Note again that Lloyd Morgan has no particular focus on behavior. In fact, he is here specifying ‘bodily tissues’, which is odd for reasons that will become manifest as my argument unfolds. The point is that environmental change is pivotal to Baldwin and Lloyd Morgan’s idea of individual acquisition and its consequences, and it will remain a central issue for the remainder of this discussion.

The basic logic of Baldwin/Lloyd Morgan on individual acquisition is simple, and deserves to be unpacked. In any stable and consistent environment, there is a classic fit between itself and the form and function of its inhabitants. If the environment changes drastically, the survival value of this same form and function diminishes, placing the inhabitants at great risk. Under these new conditions, they must adopt new form/function in order to survive. It follows that those whose form/function is rigidly fixed will likely perish, while those whose form/function is plastic and adaptable will fare much better. Under changing environmental conditions, ontogenetic plasticity is therefore the key to survival. Ultimately, this gives environmental change a special status as a stimulus for pronounced evolutionary effects.

Of the major advocates of the Baldwin effect, beside Baldwin himself and Lloyd Morgan, the one who really does justice to individual acquisition is Terrence Deacon. He states that “Behavioral flexibility enables organisms to move into niches that differ from those their ancestors occupied” (1997, p. 322). Note that he is talking about environmental change, although here the change is determined by the movement of organisms themselves. More on this later. But more importantly, he is stressing ‘behavioral flexibility’, the type known as learning. Contra Lloyd Morgan, Deacon regards learning as the essential plasticity that allows organisms to cope with change:

Of all the forms of adaptation, the flexibility to learn new behavioral responses during one’s lifetime can produce the most rapid and radical evolutionary consequences. Indeed, the ability to learn and thus inherit acquired behaviors may be one of the most powerful sources of evolutionary change. It provides an organism with access to a repertoire of *potential* adaptations, and so amplifies and extends the range of the behavioral predispositions that can be “sampled” by natural selection (p. 326, author’s own emphasis).

Now this passage is being taken somewhat out of context, because he then goes straight into the hereditary replacement that follows, but that is the point. It is difficult to say how seriously Deacon himself takes individual acquisition in isolation, rather than relying on hereditary replacement to bear the weight of his words. Nonetheless, it is my claim that the general message of the above passage can easily be understood and appreciated in terms of the sheer evolutionary significance of acquired behavior, irrespective of what becomes of the behavior itself.

At this point, it is appropriate to state and qualify the distinction being made in this discussion between behavior and morphology. Roughly speaking I use ‘behavior’ to designate the use of muscles as directed by neurons, especially in the brain. I use ‘morphology’ to denote general size, shape, and mechanical structure and composition. How far an owl can physically rotate its head is morphology. The degree to which it actually happens to do so is behavior. While there is a necessary element of idealisation taken for granted, it is adequate for our purposes.

We can state Deacon’s point about flexibility in another way. A change in environment alters the criteria for likely survival, rendering previously neutral (at best) characters advantageous. Essentially, environmental change creates advantages. These advantages depend upon variation. Now suppose a dichotomy wherein advantages can be found in superior morphological fit to the changed environment, or alternatively in behavioral fit. Which one will matter more will depend on which one has the greater variation. Deacon clearly believes that behavior is far more plastic, and thus more variable, than morphology. This position is certainly not controversial. But what is implicit, and should be made clear, is that in such situations we should expect learning to play a leading role in the rapid adaptation that must occur for survival. Put crudely, one can more easily change a habit overnight than change a morphological structure! The importance of learning should be proportional to the

extent of environmental disruption. This behavioral revolution then paves the way for morphological adaptation, which follows behind at its own pace.

A further refinement of this argument is provided by Gilbert Gottlieb, who grants behavioral plasticity a dual significance. Not only does it allow an organism to “survive by behavioral means in a drastically changed environment” (2002, p. 181), it also makes it more *likely* to confront a changed environment in the first place through exploration and migration.

The central line of argument here developed can be summed up as follows. First, Baldwin and Lloyd Morgan point out that environmental change favours plasticity. Second, Deacon points out that the greater plasticity must lie in behavior rather than morphology, which means learning. And third, Gottlieb clarifies that behavior not only *responds* to environmental change, but also precipitates it. I shall henceforth refer to these points together as ‘the individual acquisition argument’. In the Baldwin effect literature, which purports to discuss the evolutionary role of learning, this argument exists only in obscure and fragmentary form. It is ironic, then, that the argument has also been comprehensively laid down and defended in a completely different context, well removed from all the controversy. Although not framed in the rhetoric of how learning guides evolution it still amounts to exactly that. Perhaps it is also ironic that the argument comes from a figure that the participants of the Learning and Evolution debate would probably not have expected: Ernst Mayr.

The best starting point for Mayr is an article, published in 1960, in which he explains the emergence of evolutionary novelty. He begins with a ‘tentative’ working definition of evolutionary novelty as “any newly acquired structure or property which permits the assumption of a new function” (1960, p. 351). He then focuses his discussion on the origin of structures in the sense of ‘morphology’ as used above. He lists and describes some ways in

which a new structure might originate, the most important of which turns out to be ‘change of function’. The modern lung, to cite a classic example, has its origin in the breathing function adopted by the swim bladder of some fishes. He then turns to the fundamental drive of evolutionary novelty: environmental change. In contrast to the ‘storm and stress’ orientation of Baldwin and Lloyd Morgan, Mayr gives most of his time to habitat change precipitated by the organisms themselves. Incidentally, his argument here does start to sound like niche construction: “The active shift of an organism into a novel niche or entirely new adaptive zone will set up a powerful array of new selection pressures” (p. 368).

These ‘new selection pressures’ turn out to be an important theme in his discussion of behavior:

It is now quite evident... that the evolutionary changes that result from adaptive shifts are often initiated by a change in behavior, to be followed secondarily by a change in structure... It is very often the new habit which sets up the selection pressure that shifts the mean of the curve of structural variation (p. 371).

He then sets out to illustrate this principle with the example of a population of fish evolving stronger and flatter teeth following an acquired habit of eating small snails. He then states that “[i]n view of the ever present genetic variation, it is virtually a foregone conclusion that the new selection pressures (owing to the changed habit) would soon have an effect on the facilitating structure” (p. 371). This is Mayr on the predominance of behavior in responding to environmental change. But recall that behavior can also lead the way in causing that change in the first place. On this point, Mayr is also very strong: “With habitat selection playing a major role in the shift into new adaptive zones and with habitat selection being a behavioral phenomenon, the importance of behavior in initiating new evolutionary events is self-evident” (p. 372). In his conclusion about evolutionary novelty, Mayr brings both of these ideas together into a single statement: “The selection pressure in favor of the structural

modification is greatly increased by a shift into a new ecological niche, by the acquisition of a new habit, or by both” (p. 377-8).

In a more recent article published in *American Scientist* in 1974, Mayr gives the individual acquisition argument a much more complete theoretical framework which will help us understand its implications. The most crucial element in this framework, and the main extension upon his earlier discussion, is the distinction between closed and open programs governing behavior. After describing the problems with nature/nurture style thinking, Mayr suggests it is more useful to think in terms of a genetic program which ultimately governs any given behavior. In a closed program, a behavior is rigidly encoded in the organism’s genes, effectively unlearned and inherited. In an open program, a behavior is allowed to incorporate more specific information about the ever-changing environment by means of the organism’s experience. The open program is Mayr’s way of thinking about learning. In the second part of our discussion this framework will be dispensed with, but for now we will retain it in order to be clear about Mayr’s own argument and its consequences. The strength and relevance of the individual acquisition argument is best demonstrated by stating it in the most conservative terms possible, to show that it does not depend on revisionism.

Mayr provides a second important frame of reference by taxonomising behavior into a few broad categories. The two main ones he talks about are ‘intraspecific behavior’ and ‘noncommunicative behavior’. Intraspecific behavior includes courtship and other displays exchanged between members of a social species. Noncommunicative behavior deals with other components of the environment, both animate (e.g. prey) and inanimate (e.g. dwelling). Significantly, the most studied of these turn out to be food and habitat selection, exactly the sort of behavior he discusses above with respect to evolutionary novelty. Mayr claims that intraspecific behavior is generally based on a closed program. Since courtship rituals are a way of preventing cross species-fertilisation and the resulting breeding failures, for example,

they should be highly stereotyped and precise. This means that the greater flexibility of an open program would be disadvantageous. In contrast, noncommunicative behavior is generally based on an open program. This is because “[f]ood sources come and go and so do competitors. Habitats change and an individual will encounter different substrates. Phenotypic flexibility rather than genetic precision is at a selective premium under these circumstances” (1974, p. 656).

This paves the way for a concluding section titled ‘Macroevolutionary Consequences.’ Mayr concludes that as far as behavior goes, “[n]oncommunicative behavioral shifts in the utilization of the animate and inanimate environment are by far the most important factors in macroevolution. They are involved in all major adaptive radiations and in the development of all major evolutionary novelties” (p. 657). And this, of course, is the form of behavior whose underlying genetic program is generally open:

noncommunicative behavior leading to an exploitation of natural resources should be flexible, permitting an opportunistic adjustment to rapid changes in the environment and also permitting an enlargement of the niche as well as a shift into a new niche. Such flexibility would be impossible if such behavior were too rigidly determined genetically (p. 657).

Note how ‘opportunistic adjustment’ and the niche statements respectively specify both the ‘response to change’ and ‘cause of change’ functions of behavior with respect to the environment. Also, here Mayr makes a statement closer to the ‘storm and stress’ emphasis of Baldwin and Lloyd Morgan. For all intents and purposes the entire individual acquisition argument is all there, only this time it has come out of the heyday of classic mid-century evolutionary biology.

With the paper just discussed, however, Mayr presents his own important additional consideration: the distinction between behavior that is genetically determined (closed

program) and that which is open to modification via experience (open program). This distinction represents the classic nature/nurture problem, albeit in a very conservative way. However, even in this conservative form, the nature/nurture problem is the key to revealing just how important learning really is to evolution. The difference between an open and closed program is a matter of ontogeny, or to use Mayr's famous terminology, a 'proximate' problem concerned with the reading, not the writing, of the genetic program. Phylogeny, or 'ultimate causation', is about the writing of the program, whereby the selection of alternate alleles determine what sort of program is to the average individual's greatest advantage. Retaining the crude idea that morphological structure is non-plastic (an assumption we will refine later), the nature/nurture problem would indeed be a merely proximate one if selection merely acted on morphological structure.

But what happens when selection operates on behavior, which itself is the product of an open program? What happens is that the significance of the open/closed distinction extends from ontogeny into phylogeny, creating a logical pathway to a form of anti-reductionism. If an individual acts according to a closed program and is rewarded by selection, the genes it passes on to its offspring contain the program for that same behavior. Consequently, that behavior will continue into the next generation *because of* the benefit it provided to the parent. In a very real sense the behavior that occurred has been selected because it is reducible to the genes that encoded it. But when an individual is rewarded for a particular behavior performed in accordance with an open program, all that is passed on genetically to the offspring is the learning mechanism that *allowed* the behavior to occur. The offspring will inherit that mechanism *because of* the benefit it provided to the parent. But whether or not the offspring repeat that behavior is by no means reducible to the genes. There is no real sense in which truly Darwinian selection has acted on the behavior that actually occurred under the open program.

This means that, according to the individual acquisition argument, it is not actually the *genetic basis* of behavior that plays this key causal role in the course of evolution, but rather the *actual behavior*. Although the ability to learn is genetically encoded such that it can be passed on, the evolutionary trajectory of a learning species cannot be understood just in terms of this hereditary aspect of learning, without references to the learning that actually occurs. There is a very simple sense in which animals can be said to make ‘choices’, irrespective of whether they ultimately reduce to chance or determinism. That is, an individual of a population in a given situation could theoretically be expected to act in one of several ways within its typical set of constraints, but for whatever reason behaves one way rather than another. In the open program, this choice is the result of a lifelong interaction between a learning mechanism and the stimuli it encounters, a history which is not directly written in the genes. These choices can be the beginning of a chain of evolutionary events, themselves reducible only in the trivial sense that they have operated within a biological system in an environment, both emerging from the nature of chemistry, quantum mechanics, etc. Learning creates an especially potent element of contingency wherein actual behaviors, rather than behavioral programs, can be as causally relevant to evolution as selection upon variation. Just as an instance of learning might be necessary or utterly unable to explain an instance of selection, so an instance of selection might be necessary or utterly unable to explain an instance of learning. Yet, both processes have evolutionary consequences.

Mayr spells out the importance of behavior, namely learned behavior, in evolution rather comfortably, but stops short of its logical implications. Gottlieb points out that “[a] very important theoretical component of the modern synthesis is the idea that some organismic variation is heritable and some is not heritable and it is only the heritable variation that is significant for evolution” (p. 122). This statement seems irreconcilable with Mayr’s view, which has learned i.e. non-heritable behavioral variation essentially trailblazing life through

macroevolution. That being said, it would be premature to state conclusively that the individual acquisition argument has any direct bearing on the Modern Synthesis. But it does raise a number of inter-related questions. Does learning present a demonstrable case of anti-reductionism relative to traditional evolutionary thinking? Does Mayr's argument show that the Modern Synthesis view is not always compatible with the product of its own mechanics? How do we understand the Modern Synthesis, and how it understands itself, in terms of the type and extent of its claims and principles? It is too easy to produce counter-examples to careless rhetoric about the total irrelevance of the non-heritable, the proximate etc.. It is beyond the span of this paper, though, to adequately address the issues I have just raised. That would require a detailed and fair assessment of Modern Synthesis theory and a proper philosophical inquiry into the precise logical consequences of individual acquisition. My own outline of the apparent causal significance of learned behavior is merely a starting point.

3. Where Individual Acquisition Stands Today

Up until this point, the focus of this discussion has been historical. The point has been to unpack an argument that not only already exists, but does so in the very literature where it should have been recognised in the modern debate over learning and evolution. This historical orientation is conservative, because the evolutionary significance of learning is a problem of far greater scope than what can be pointed to in literature selected for such a particular historical aim. In order to consider this greater significance properly, it is necessary to remove it from the boundaries imposed by the historical interest in Mayr and the Baldwin effect literature. In the remainder of this discussion, I will therefore leave this historical interest behind and instead offer a brief contemporary review of just how important learning might be as a factor in evolution.

The starting point of this review is the individual acquisition argument. Overall, this argument has been stated in such general terms in the literature above that it hardly needs modification. The historical survey of the argument given above can thus be treated as a detailed explication of an argument whose logic remains entirely relevant, and in my view, perfectly convincing. There is but one significant limitation that the historical framing has imposed upon the argument so far: it was considered in terms of Mayr's genetic program concept. This is a controversial premise and may prove untenable, so reliance upon it would render the individual acquisition argument rather vulnerable. Fortunately, the genetic program concept is completely dispensable. All that the argument really depends on is that an animal's behavior can depend significantly on learning i.e. the effects of environmentally imposed experiences on the likelihood of certain behaviors. The open genetic program was merely Mayr's preferred version of that basic principle. The anti-reductionist argument I drew from Mayr could just as easily have been based, for example, on operant conditioning.

The potential enhancement of the individual acquisition argument does not stop with the extraction of the genetic program. Gottlieb has effectively taken the argument further. He does this in two ways. First, recall his point that behavior can both respond to and precipitate environmental change. He specifies a mechanism for both phenomena based on behavioral neophenotypes, "momentous behavioral changes or deviations from normality that could be brought into existence by altering the usual conditions of an animals' [sic] early development or experience" (p. 175). Enhanced stimulation at such early stages leads to enhanced behavioral plasticity in adulthood, stimulating exploratory behavior and the ability to adapt to the consequent changes. He further correlates this capacity with brain size, arguing that the comparatively larger brains of the higher vertebrates (birds and mammals) relative to body size renders them more plastic, and therefore more adaptable.

The second way in which Gottlieb enhances our picture is his three stages of evolutionary change. Stage I is ‘change in behavior’, i.e. individual acquisition. Stage II is ‘change in morphology’. This is the key point made above, that the greater plasticity of behavior gives it a leading edge over morphology, which must catch up afterward. The real novelty comes with stage III: ‘change in genes’ (p. 177). Gottlieb recognises the massive stock of unused (unexpressed) genetic material in the genome, and claims that this can easily be utilised to induce morphological modification via changes in the developmental system. When a population has moved to a new environment and successfully adapted with new behaviors, the resulting selection pressure on morphology does not act on differential genotypes, but rather on differential phenotypic expression. Under this epigenetic scenario, change in genetic composition, even at the population level, is not necessary. Genomic evolution can result, but by the time it does the evolution on the phenotypic level has already come to pass. Genomic evolution is Gottlieb’s stage III, the final stage in evolutionary change, if indeed it actually occurs at all, which it might not. Gottlieb points out that according to the Modern Synthesis perspective, which defines evolution precisely as a change in the genetic composition of the population, the morphological adaptation of stage II does not count as evolution at all, but actually precedes evolution (stage III) (pp. 193-4).

I have argued that the significance of learning for evolution has been conflated with the Baldwin effect, or hereditary replacement. Having separated these, I have focused on learning in the form of the individual acquisition argument, and in doing so have ended up with a conflation of my own. I now want to move beyond this, in two fundamental and complementary ways. First, the individual acquisition argument is a behavioral version of a broader phenomenon, applicable to other (morphological) forms of plasticity. Second, there are other ways in which learned behaviors can relate to evolution (again without resorting to the Baldwin effect). In a word, there is more to the individual acquisition argument than

learning and more to learning that the individual acquisition argument. Both points will be made in turn, both drawing from the extensive treatment of the general subject by West-Eberhard.

In her monumental work *Developmental Plasticity and Evolution*, West-Eberhard sets out to synthesise a theory of evolution which properly incorporates the phenotype, arguing that an understanding of biological organisation, which involves developmental plasticity, is essential for an adequate understanding of evolution by natural selection. She emphasises that “[a]daptive evolution is a two-step process: first the generation of variation by development, then the screening of that variation by selection” (2003, p. 139). From this vantage point, she proposes four fundamental processes involved in adaptive evolution (p. 140). The first of these is the appearance of a novel trait, arising from an alteration of a pre-existing phenotype. For the individual, this is followed by the second process, ‘phenotypic accommodation’. This is the adjustment of the phenotype as a whole to the novel trait. It is classically illustrated by the example of a mutant goat which, born without forelegs, developed bipedal behavior and physiology, and hence known as the ‘two-legged goat effect’ (pp. 51-4). The third process (or principle) is recurrence. This means that whatever factor stimulated the novel trait effects many individuals, resulting in “a subpopulation of individuals that express the trait” (p. 140). Alongside heritability, recurrence is a prerequisite for natural selection (pp. 142-3), and its traditional form is the initial spread of a genetic mutation. Finally, the genome itself adjusts to the change, a process called ‘genetic accommodation’.

According to West-Eberhard, there are two likely factors which can initiate a novel trait: genetic mutation and environmental induction (p. 145). She argues, radically, that the latter is actually the superior agent of adaptive evolution. She provides several reasons for this, but I will focus on two of these which are simple, complementary and arguably fundamental. They relate to the importance of recurrence, described above. They are also based on the principle

of interchangeability, which means that the switches that determine development on the molecular level are susceptible to inputs of both genomic and environmental origin. These inputs can be mutually substituted resulting in phenocopies, “environmentally induced mimics of genetically specified traits” (p. 116), and/or genocopies, where the latter mimic the former. Thus: “The developmentally plastic phenotype can respond to both genetic and environmental inputs... This gives the environment a foot in the door of evolutionary innovation” (pp. 503-4). One key reason that environmental inputs are superior to genetic ones is that recurrence can be achieved much more easily. A change in an environment can potentially effect an entire population in a single generation. A random genetic mutation, in extreme contrast, must first spread from a (very likely!) single individual into the population over several generations. Basically, it has a long way to go to achieve recurrence, and to do so it must survive. This relates to the second basic reason environmental induction is superior: it is relatively immune to selection. Even a hostile environment will not be selected out of existence somehow because it impeded the survival of its inhabitants, whereas a genotype with the same effects will be expected to perish with its unfortunate carriers.

This is the theoretical background against which West-Eberhard emphasises the capacity of phenotypic plasticity to produce novelty under environmental stress. This same stress is also the basis of the relevant selection pressure:

An extreme environment implies strong selection as well as extreme phenotypic responses. When an environmental contingency is both recurrent and extreme, ... one expects to find both coordinated expression of environmentally sensitive responses and particularly strong *selection* on the responses, both due to the extreme environment itself (p. 506, italics in original).

It should be made explicit that the very extremity of such an environment and its function as a source of both phenotypic stress and selection pressure imply that life is still in the process

of adapting. That is, it implies that the conditions are relatively new; it implies significant environmental change.

The individual acquisition argument is also about plasticity, but regards behavioral plasticity as superior to that of morphology. Now, we can frame the evolutionary consequences of individual acquisition in more general terms inclusive of West-Eberhard's argument. A change in environment presents an immediate advantage for plasticity. The novel traits that result are thereby environmentally induced. In future generations this is followed by other adjustments which take their time. This is the process West-Eberhard calls genetic assimilation. The individual acquisition argument is admittedly more crude, didactically identifying the plastically derived novelties with behavior and the following more drawn out processes with morphology catching up. Although this is clearly idealistic and ignores the bigger picture of more general phenotypic plasticity, it is arguably still a formidable case for the importance of learning. It is this emphasis on learning that sets it apart from West-Eberhard's argument above, although she does address learning in a different way, as we shall see.

In her discussion of learning, West-Eberhard actually does briefly treat learning as a particular case of her more general argument, in a section titled 'The Genetic Accommodation of Learned Traits' (p. 339). After pointing out the value of learning in 'producing trait recurrence', she claims that "learned traits have a greater evolutionary potential than do mutational ones, since many individuals of a population may simultaneously and suddenly learn the same things in the same circumstances, or due to mimicry of other individuals" (p. 339).

The comparison of West-Eberhard's general argument with the individual acquisition argument also helps us appreciate the extent of the irony of Mayr's acceptance of the latter.

In her discussion of environmental stress and its phenotypic consequences in producing novelty, West-Eberhard comments on the maximal general resistance to environmental induction in the 1950's and 1960's. She provides a delightful quote from Mayr: “the early Mendelians... misinterpreted just about every evolutionary phenomenon. Some of their contemporaries... *even believed in some environmental induction*” (Mayr, 1963, cited in West-Eberhard, p. 505, my emphasis). How can behavior which is produced by an open genetic program, which by definition allows behavior to be shaped by environmental feedback, not be considered environmentally induced?

On the topic of learning in evolution, West-Eberhard takes a position very similar to my own. She too notes that

[i]n the past, evolutionary discussions of learning and evolution have tended to emphasise either the idea that learning ability is the thing that evolves, or the idea that learned traits can be genetically assimilated – the idea that a ‘genetic’ or constitutively expressed trait can begin as a learned one” (p. 338).

For West-Eberhard, there are two “general relationships between learning and genetical evolution” which are more important than these, and they will now be described in turn.

One of these relationships is that learning functions as a ‘Fitness-Effect Screening Device’:

When learning involves evolved motivational cues and reward criteria, it imposes a fitness-effect assay on behavioral decisions. Motivations and rewards molded by natural selection provide a built-in means of trial-and-error screening for those behaviors that are likely to have positive fitness effects, leading to the repetition of those likely to be beneficial to the organism (p. 339).

West-Eberhard is stressing a correlation between the behaviors that are learned and those that benefit the organism, and she criticises previous discussions for missing this correlation. The

‘framework of genetics’ allegedly focuses only on the transmission of behaviors across generations, irrespective of whether or not these behaviors benefit their subjects. In particular, she cites Dawkins’ *The Selfish Gene*, evidently identifying learned behaviors with his ‘memes’.

But Dawkins, in the same book, seems to make the same argument that she does. In his chapter on ‘The Gene Machine’, Dawkins states that “[o]ne way for genes to solve the problem of making predictions in rather unpredictable environments is to build in a capacity for learning” (2006, p. 57). He describes this capacity as a program giving instructions to repeat behaviors resulting in obviously fitness-correlated experiences, and to not repeat behaviors resulting in the opposite. “The advantage of this sort of programming” he claims, “is that it greatly cuts down the number of detailed rules that have to be built into the original program; and it is also capable of coping with changes in the environment that could not have been predicted in detail” (p. 57). In other words, adjustment to the environment can be radically enhanced by allowing ‘trial-and-error’ fitness screening rather than relying entirely on the fitness-benefits of hard-wired behavior programs.

It should not be surprising that even the gene-centred Dawkins recognises this point. As important as it may be, it is difficult to see how it departs from ‘the idea that learning ability is the thing that evolves’, because it only explains how a learning mechanism enhances the fitness of an individual. Learning does indeed allow an animal to screen its behavioral repertoire and thus exhibit more fitness-positive behavioral traits in its lifetime. One can call this an ontogenetic microcosm of Darwinian selection. But what are its consequences for evolution? The answer is that the learning mechanism confers a reproductive advantage and therefore is likely to be passed on to later generations! Although it is implicit in the individual acquisition argument, the sheer fact that this particular survival mechanism constitutes a certain mirror of the fitness effects encountered in the environment does not seem to make it

any more important *for evolution* than any other survival mechanism. It does not involve itself in evolution in any special way. What is more, by limiting Dawkins' supposed appreciation of learning to his memes, West-Eberhard seems to imply that the phenomenon of learning in itself is intrinsically incongruous with traditional evolutionary theory. Such a presentation of traditional thinking is arguably a caricature.

More substantial and interesting is West-Eberhard's other point about 'learning as a developmental source of evolved correlations'. She explains this with the example of dieting in some birds: "the form and the size of the beak render some dietary choices more quickly rewarding than others" (2003, p. 338). Once this morphological feature is correlated with the feeding behavior, other physiological factors such as digestion might also be influenced. The crucial point about learning is that it plays a key role as the developmental process which links different aspects of morphology functionally together into a "coordinated, complex expressed phenotype [that] is subject as a unit to selection" (p. 338). Whereas learned behaviors are not heritable themselves, they nevertheless serve a kind of scaffolding purpose in the creation of the phenotypes that are screened by selection (recall the two processes of adaptive evolution above)

Even better, she goes on to claim that this trait-complex in turn can feed back into reinforcing the learned behavior, because the enhanced physiological fit for that behavior renders it more effective, and therefore more rewarding (p. 338). She neatly summarises the situation: "Clearly, there is a kind of circular interaction between morphology and learning in evolution, learning being influenced by morphology and the resulting learned specialization in turn influencing the direction of selection on morphology itself" (p. 339).

Before concluding, there is one further evolutionary function of learning that deserves mention. Brown (2013) has emphasised that learning can have a long-term, population level

effect on the evolution of a species. In spite of my argument, a population can, of course, survive a severe environmental disruption by rapid selection of genetic traits. However, this sort of adaptation can have a very disruptive effect on the population's gene pool. It can reduce the genetic diversity of the population, rendering it less plastic and adaptable, and compromising its ability to face new threats in the future. In this way, it reduces the evolvability of the species. In contrast, if a population is able to simply learn its way around the environmental change and thereby avoid significant genetic modification, this problem is avoided. In this way, learning can enhance the capacity of a population to preserve its genetic diversity, thereby increasing its evolvability and giving it an edge over any non-learning population (note the group-selectionist flavour here). By comparison with the discussion in the rest of this paper, this argument is somewhat conservative and does not affect the direction of evolution in the conventional sense (except of course, for the evolution of evolvability itself). It is nevertheless very interesting and adds yet another nuance to the manifold ways in which, as evolutionists, we can think about learning.

4. Conclusion

Paul Griffiths has argued that “too much attention has been paid to the Baldwin effect” (2003, p. 193). I think this statement is very true. The two most basic components of the Baldwin effect are individual acquisition and hereditary replacement. It is the latter that makes it the Baldwin effect, and which, for no evident good reason, has taken centre stage in the controversy over the evolutionary importance of learning. This is probably because hereditary replacement has a certain Lamarckian flavour, and in the history of Neo-Darwinism there seems to exist a very real fear of Lamarckian inheritance, as though there is some danger involved in even questioning the possibility.

In the history of evolutionary theory, learning, be it by that name or any other, has been discussed innumerable times. The writings considered in this paper should be seen as a sample rather than a survey. Unfortunately, all the literature out there exists only in scattered, fragmentary, unsystematic and ultimately obscure form, with people in different contexts and disciplines asking and meaning different things. What is more, all the hype about learning ‘guiding’ evolution has been dominated by the Baldwin effect. It is evident that learning has not received enough attention in evolutionary thinking. In order to rectify this, the issue and its history really need to be properly unearthed, and the fragments of theory and discussion brought into one place. In this way, we can begin to establish the coherent literature we need to think really seriously and thoroughly about what learning has to do with evolution.

There is a particular reason that the Baldwin effect fails to address this. Because learning helps determine the way an organism behaves, it is understandable that when one thinks about learning guiding evolution, there is an inclination to assume that what is meant is that learning can guide the evolution *of behavior*. But this cuts the question too short. The present discussion makes clear that learning concerns *evolution*, not just behavioral, but morphological. Because learning can take the lead in changing environments, paving the way for morphological adaptation, individual acquisition does not stop at behavior, like the Baldwin effect, but bears on evolution generally, behavioral and morphological, among all learning creatures. By granting causal power to the selection of behaviors only as predictable as their environmental context, it pulls down the curtains around behavioral/cultural evolution and implicates itself in the greater world of biological form and function, from eyeballs to skeletons.

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ⁱ This general redefinition, aimed at claiming priority against Lloyd Morgan and Osborn, is well known. However, I have seen no mention of the fact that this redefinition occurs *within* the paper discussed.

ⁱⁱ In Depew's account the above term is attributed to "one wag".